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THE ANATOMY OF A HYBRID EQUISETUM[1]

RUTH HOLDEN

The genus Equisetum has been the object of a considerable amount of study on the part of a great many botanists. As a rule, each has chosen certain features for especial investigation, with the result that each has adopted a different scheme of classification depending on what characters he himself deemed of most significance. Consequently, there is not a little divergence of opinion as to what features are of specific and what are of varietal importance. The confusion is increased by the large number of forms which differ from each other only in slight, though seemingly constant characters. For example, Mr. A. A. Eaton, who was the systematic authority on this genus in America, concluded that the true *Equisetum hiemale* L. is not found on this side of the water, but is replaced by *E. hiemale* var. *affine* (Engelm.) A. A. Eaton which differs in that the ridges of the stem are rounded instead of biangulate. As he expressed it (Fern Bulletin, v. II, p. 7) "the subgenus Hippochete is a multitude of races of which species are the centers of variation." Accordingly, he established a number of so-called varieties, which, as far as external features are concerned, bridge over by gradual steps all the gaps between different species. Thus, *E. arvense* L. grades into *E. littorale* Kühl through *E. arvense* var. *diffusum* and *E. littorale* var. *arvensiforme*. Duval Jouve (Histoire Naturelle des Equisetum de France), on the other hand, has done much to show that what have been described as separate varieties, or even separate species, are often merely fluctuations dependent on some environmental difference. For example, *E. fluviatile* L. was made a different species from *E. limosum* L. by Linnaeus, because the former has numerous branches, while the latter has none. Duval Jouve, however, claims that one grows in deep water and one in shallow, and that both species, with all the intermediate varieties, spring from the same rhizome. Milde (Monographia Equisetorum) goes further still, and considers that since *E. ramosissimum* Desf., *E. hiemale*, *E. trachyodon* A. Br., *E. variegatum* Schleich.,

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[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 65.

E. scirpoides Michx., *E. laevigatum* A. Br., and *E. robustum* A. Br. are all connected by transitional forms, they should be considered a single species. It may be possible to introduce some order into this chaos by a more careful anatomical study of these forms. As a possible first step in this direction, *E. variegatum* var. *Jesupi* A. A. Eaton has been chosen.

This variety was originally described by Eaton as "almost exactly intermediate between *E. variegatum* and *E. hiemale*," and the photographs of plate I show such to be the case. Figures 1, 3 and 5 represent respectively *E. variegatum*, *E. hiemale*, and *E. variegatum* var. *Jesupi;* figures 2, 4, and 6 the same at double the magnification. In size of stem and cone, the variety is approximately half way between *E. variegatum* and *E. hiemale.* According to Mr. Eaton, one of the best diagnostic characters is that of the sheath. In *E. variegatum*, it is loose, terminating above in persistent teeth (fig. 2). These teeth have a dark median groove, with a white border on each side, and end in deciduous awn like points. The sheath of *E. hiemale* on the other hand, is tight, with a black base and tip. The teeth are long, but articulated to the sheath and soon deciduous (fig. 4). The sheath of *E. variegatum* var. *Jesupi* is usually loose as in *E. variegatum;* like *E. hiemale* it has a black band, which in the second year reaches the base, while the upper part becomes ashy (fig. 6). The teeth are similar to those of *E. variegatum*, having the same dark median groove, and white border. Unlike *E. variegatum*, however, the awn points are usually persistent. Another fairly constant feature is the character of the ridges. This may be seen more easily in transverse sections, but it is indicated in the habit photographs. In *E. variegatum*, they are sharply biangulate, with a groove down the center of each. There is accordingly, a double row of siliceous tubercles to each ridge. Those of *E. hiemale* var. *affine*, on the other hand, are rounded, with a single row of tubercles. They may be clearly seen in figure 4. In *E. variegatum* var. *Jesupi*, the ridges are usually bluntly biangular, with rarely a carinal furrow. Like *E. variegatum*, there is usually a double row of tubercles (fig. 6).

With this brief account of the external appearance of these three Equiseta, we may turn to their internal structure. Figures 7, 9, and 11 represent respectively transverse sections of the internode of the aerial stems of *E. variegatum*, *E. variegatum* var. *Jesupi*, and *E. hiemale.* In some respects they are quite similar; all have a double endodermis continuous between the bundles; all have the sunken stomata characteristic of the subgenus Hippochaete; all have the stomata in two lines down the furrows, rather than scattered as in *E. littorale* and *E. limosum;* and all have the three sets of canals—central, vallecular and carinal. These sections corroborate the statements made above in regard to the outline of the stem. In *E. variegatum* (fig. 7) the ridges are sharply biangulate with a carinal furrow. Often in *E. variegatum* var. *Jesupi* (fig. 9) they are rounded, though not infrequently, bluntly angled. In *E. hiemale* (fig. 11) on the other hand, they are always rounded. These three photographs show also the relative size of the canals. The central and vallecular canals of *E. variegatum* have approximately the same diameter; in *E. variegatum* var. *Jesupi*, the central is considerably larger; and in *E. hiemale* this is still more the case.

Next to the distribution of the endodermis, the character of the bast fibers, with its consequent effect on the distribution of the green parenchyma, has been considered by anatomists as the most important diagnostic feature. In *E. variegatum*, there is a considerable mass of these fibres under both ridges and furrows, but it is usually heavier in the latter position. It extends inward to the border of the vallecular canal, thus cutting the green parenchyma at that point. This interruption of the palisade tissue under the furrows and its continuity under the ridges, seems to be invariable in *E. variegatum*, though Milde figures it as continuous around the whole stem. In *E. variegatum* var. *Jesupi* on the other hand, there is no such constancy. The carinal bast is usually more extensive than the vallecular, but, even so, the palisade tissue is not uncommonly continuous under it. Figure 8 shows a section where such is the case. The masses of vallecular bast are relatively small, but usually they reach the jacket of cells which surround the canals. This variability results in the green parenchyma being sometimes interrupted at only the furrows, sometimes at only the ridges, sometimes under both ridges and furrows (fig. 10), and rarely being continuous around the entire stem. Not infrequently, due to some irregularity, the carinal bast is pushed to one side of the ridge, and a similar displacement may occur to the vallecular. Toward the upper left of figure 9 instances of both these may be seen. Such a condition is at variance with Eaton's description. He saw the interruption of the green parenchyma by the carinal bast, but failed to see that by the vallecular. Inasmuch as the writer has had access to material from a number of different localities, some of which was identified by Eaton himself, it seems as though the error must be his. Figure 11 shows these structures in *E. hiemale*. According to Eaton, Duval Jouve, and Milde, the carinal bast in this species is the better developed, and interrupts the green parenchyma under the ridges, while it is continuous under the furrows. If figure 11 be examined with a hand lens, however, it will be found that while the masses of bast fibers at the ridges are larger than those at the furrows, there are invariably, as in *E. variegatum* var. *Jesupi*, cells extending inward from the latter which cut across the palisade tissue at that point, also. Figure 12 shows a small portion at a higher magnification, and there can be no doubt that such is the case. This section was cut from material grown in Toronto, Ont. On the other hand, plants grown in Cambridge, Mass., presented usually the conditions which have been described as typical for the genus—the parenchyma is continuous under the furrows.[2] The importance of these discrepancies is not necessarily great, Milde himself having found considerable variation throughout the genus, and especially in *E. hiemale*.

With this description of the aerial stems of the three Equiseta, it is clear that *E. variegatum* var. *Jesupi* occupies a position somewhat intermediate between the other two. Its bluntly biangled ridges are half way between the rounded ones of *E. hiemale* and the sharply angled ones of *E. variegatum;* while in the distribution of bast fibers and green parenchyma, it has the vallecular interruptions common to both the others, and the carinal interruptions of *E. hiemale*.

In the structure of the rhizome, there is also considerable divergence among the three. Figures 13, 15 and 17 represent respectively transverse sections of the internode of the rhizomes of *E. variegatum*, *E. variegatum* var. *Jesupi*, and *E. hiemale*. As in the aerial stems, the central canal of *E. hiemale* is much larger in proportion to the vallecular, than is the case with either of the others. The endodermis of *E. variegatum* has the same distribution in the underground as in the aerial stem—it is double, and continuous internally and externally. The endodermis of *E. hiemale*, on the other hand, is like that of *E. variegatum* in the aerial stem, but in the rootstock, it forms a separate sheath around each bundle as in *E. limosum.* In this respect, *E. variegatum* var. *Jesupi* is like *E. variegatum,* having a common internal and external sheath. Another feature of resemblance to *E. variegatum,* on the part of *E. variegatum* var. *Jesupi,* consists in the absence of socalled "nodal organs." These parenchymatous swellings, probably akin to lenticels, are as Dr. Jeffrey has pointed out (Structure, Development and Affinities of the genus Equisetum) present in *E. hiemale,* and lacking in *E. variegatum.* They seem to be absent also in *E. variegatum* var. *Jesupi.* Accordingly, as far as rhizome is concerned, *E. variegatum* var. *Jesupi* is considerably more like *E. variegatum* than *E. hiemale.*

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[2] Since writing the above, I have had an opportunity of investigating the stems of *E. hiemale* from Niagara Falls, Canada, and from the Cambridge, England, Botanical Gardens, and in all the specimens have found the green parenchyma continuous under the furrows.

Another fairly constant feature is the nature of the diaphragm, which occurs immediately above the node of both aerial and underground stems. Figure 14 shows a transverse section of *E. variegatum,* and figure 19, a longitudinal one. It is evident from these two photographs, that the upper surface of this diaphragm is covered with a layer of very thick walled, darkly staining cells. These are the tannin cells. They usually occupy the entire pith at this point, and also form large masses immediately inside the vascular bundles, extending upward for a considerable distance. Beneath them, are thinner walled, parenchymatous elements, which, toward the centre, show a tendency to become arranged in longitudinal rows. In *E. variegatum* var. *Jesupi,* the conditions are different, in that the tannin cells are considerably less in extent. Instead of occupying the entire pith, they appear in only a part of it (fig. 16). They are not equally developed in every node, so that, especially in the aerial stem, a longitudinal section may miss them altogether (fig. 21). On the other hand, the cells beneath are in distinct, longitudinal rows, forming a true periderm. As in other respects, *E. hiemale* goes one step beyond *E. variegatum* var. *Jesupi.* The tannin cells (fig. 18) occur only in isolated masses, and often, even in the rhizome, they fail to appear at all (fig. 23). The periderm, however, is very well marked, two or three layers of cells being lignified. Thus in the development of tannin cells and of nodal periderm, *E. variegatum* var. *Jesupi* is intermediate between *E. variegatum* and *E. hiemale.*

Finally, the cones of these three Equiseta were examined. Figure 20 represents a section of *E. variegatum.* In the centre is the sporophore, above and below which are the sporangia. The uniform size of the spores and their elaters coiled around them, are easily distinguished. The character of the wall may be best seen in the case of the two lower sporangia. It is one cell thick, and the cells themselves are covered with spiral thickenings. According to Duval Jouve, these spirals are characteristic of all species of Equisetum except *E. littorale* and *E. trachyodon.* Figure 24 represents a section of a cone of *E. hiemale,* including parts of four sporangia. Owing to defective technique, the spores are somewhat shrunken, but examination of fresh material, shows that all are spherical and all are uniform in size. Even in the section, the elaters appear clearly, and also the spirals in the walls. Figure 22 represents a single sporangium from a cone of *E. variegatum* var. *Jesupi.* Unfortunately the same shrinkage has taken place as in the cone of *E. hiemale,* but, despite that, it is evident that while some spores are normal in size, many are much smaller. The former always have elaters, while the latter often lack them. A further peculiarity is that the sporangium wall never has spirals. Through the kindness of the authorities at the Gray Herbarium of Harvard University, an opportunity was afforded to examine the cones of a number of specimens from eastern Canada and New England, including the type specimen from Royalton, Vermont, and in all the same mixture of normal and abnormal spores was found.

To sum up, *E. variegatum* var. *Jesupi* is like *E. variegatum* in the sheath with persistent teeth, in the location of the endodermis, in continuity of green parenchyma under the keels (rarely), and in absence of nodal organs in the rhizome. It is like *E. hiemale* in the black band of leaf sheath, and in the interruption of green parenchyma at both ridges and furrows (usually). It is intermediate between the two in height and diameter of stem, outline of ridges, relative size of vallecular and carinal canals, occurrence of tannin cells, and development of nodal periderm. Further, a large number of the spores are abortive, and the sporangium wall lacks spirals.

Before considering the significance of these facts, it may be apposite to recall the conditions in another member of the same genus, *E. littorale.* According to Milde, this species is like *E. arvense* in the constant presence of two rows of canals, in the presence of tubercles, and often in the form and color of the sheath; it is like *E. limosum* in the stomata, in the absence of a carinal furrow, in the teeth of the leaf sheath, and often in the form and color of the sheath. It is intermediate in the form of the green parenchyma which is sometimes like *E. arvense* and sometimes like *E. limosum;* in the cone axis which is neither hollow like the latter, nor entirely solid like the former; and in the central cavity which is half way between the two. Further, the spores are always partially abortive, and the sporangium wall lacks spirals. Milde, in company with most other authorities, has concluded from this evidence that *E. littorale* is a hybrid between *E. limosum* and *E. arvense*. Exactly the same arguments are applicable to *E. variegatum* var. *Jesupi*, which must be a hybrid between *E. variegatum* and *E. hiemale*. The presence of abortive spores, and absence of spirals in the walls of the sporangium seem to be reliable indications of hybridization, the present writer having found exactly the same conditions in a cross between *Betula pumila* and another birch.

It seems obvious from this evidence that *E. variegatum* var. *Jesupi* is clearly a hybrid, occupying an intermediate position between *E. hiemale* and *E. variegatum*. The question then arises whether it is the first filial generation of this cross. Before attempting to answer, there are various other facts to be considered. First, what is the relation of *E. variegatum* var. *Jesupi* to the European *E. trachyodon*? The latter is likewise considered by Alexander Braun to be intermediate between *E. hiemale* and *E. variegatum*, and indeed there are similar arguments for its hybrid nature as for that of *E. variegatum* var. *Jesupi*. Both have abortive spores, and both have a combination of the characters of *E. hiemale* and *E. variegatum*, but the combination is different. Each has a loose sheath with persistent teeth, but the bast of *E. trachyodon* is variable. According to Duval Jouve, the green parenchyma is interrupted under both ridges and furrows, while according to Milde, it is sometimes interrupted at only the ridges, and at others it is continjous around the whole stem. Moreover, while *E. variegatum* var. *Jesupi* has the endodermis characteristic of *E. varigatum*, *E. trachyodon* has that of *E. hiemale*, and further, *E. trachyodon* has the ridges of the stem biangulate, with a distinct carinal furrow. This last difference is discounted by the fact that the European *E. hiemale* has bluntly biangulate ridges, while ours has them rounded. Secondly, what relation do these varieties bear to *E. hiemale* var. *pumilum*, which Eaton considers intermediate between *E. hiemale* and *E. variegatum* var. *Jesupi*, or to *E. hiemale* var. *doelli*, which Milde considers intermediate between *E. hiemale* and *E. trachyodon?* A similar difficulty exists if *E. littorale* is a hybrid between *E. limosum* and *E. arvense:* where do *E. littorale* var. *arvensiforme* and *E. arvense* var. *diffusum* belong?

There are three possible answers: Either, as has been shown to be the case in birch crosses, the F_1 is very variable, so that some individuals are like one parent, and others like the other; or some, instead of being members of the first filial generation, are the result of long continued crossing and back crossing. The first explanation has one objection —why should *E. trachyodon* always be produced on the other side of the water, and *E. variegatum* var. *Jesupi* on this? Another difficulty is our ignorance of the way in which these infertile hybrids reproduce themselves. Are some of the spores capable of germination, or does the crossing have to take place anew for each individual? Although certain of the large spores are apparently normal, Duval Jouve, who had no difficulty in artificially cultivating other species of Equisetum, was unable to do so in the case of *E. littorale*. Furthermore, Milde has called attention to the fact that these supposed hybrids always grow in the vicinity of the parents.[3]

None of these points can be settled conclusively at the present time. The facts indicate that *E. variegatum* var. *Jesupi* is a hybrid between *E. variegatum* and *E. hiemale*, but until the cross is actually made under artificial conditions, the exact relation must remain uncertain. The genus Equisetum will be however a particularly favorable one for experimental work, since the various species are distinguished by a comparatively large number of clean cut and constant anatomical characters. Whether they are dependent on unit factors which are capable of independent segregation and recombination will be an extremely interesting and important subject for investigation.

SUMMARY.

1. *Equisetum variegatum* var. *Jesupi* is probably a hybrid between *E. variegatum* and *E. hiemale* for the following reasons: (1) It has some of the characters *E. variegatum*, some of those of *E. hiemale*, and some which are intermediate between the two. (2) A large number of its spores are always abortive.

2. Whether it represents the immediate offspring (F_1) of the cross, its relation to other varieties also intermediate between *E. variegatum* and *E. hiemale*, whether the cross is repeated for each individual, how far hybridization will explain the large number of transitional forms in

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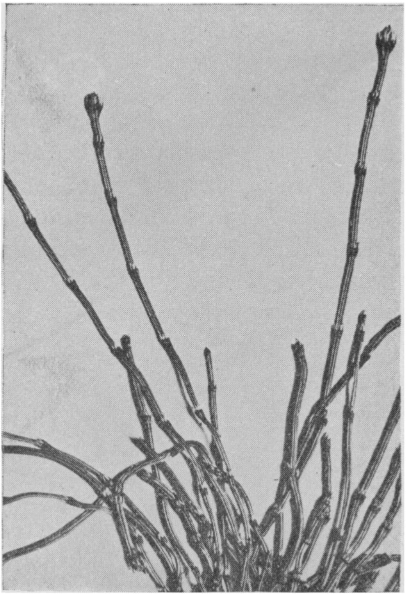
[3] A third explanation would be that instead of the result of crossing two species, three or even four may be implicated. Brainerd (Rhodora, March 1906) found indications of such complications in his work on violets, and cites one, *Viola* (*hirta* × *odorata*) × *V. collina*, from the Tyrol.

the genus Equisetum, are all points to be cleared up by further investigation.

In conclusion, I wish to express my best thanks to Professor Jeffrey for suggestions in regard to this work, and for material of *E. hiemale* and *E. variegatum* var. *Jesupi* from Toronto; and also to the authorities of the Gray Herbarium of Harvard University for material of *E. variegatum* and *E. variegatum* var. *Jesupi*, and for the loan of herbarium sheets from which the photographs of plate I were made.

EXPLANATION OF PLATES V–VIII

FIG. 1. Equisetum variegatum. × 1.
FIG. 2. Same. × 2.
FIG. 3. E. hiemale. × 1.
FIG. 4. Same. × 2.
FIG. 5. E. variegatum var. Jesupi. × 1.
FIG. 6. Same. × 2.
FIG. 7. E. variegatum, transverse section of aerial stem. × 60.
FIG. 8. E. variegatum var. Jesupi, transverse section of aerial stem. × 125.
FIG. 9. Same. × 30.
FIG. 10. Same. × 125.
FIG. 11. E. hiemale, transverse section of aerial stem. × 15.
FIG. 12. Same. × 125.
FIG. 13. E. variegatum, transverse section of internode of rhizome. × 60.
FIG. 14. Same, at node. × 60.
FIG. 15. E. variegatum, var. Jesupi, transverse section of internode of rhizome. × 60.
FIG. 16. Same, at node. × 60.
FIG. 17. E. hiemale, transverse section of internode of rhizome. × 15.
FIG. 18. Same, of node. × 15.
FIG. 19. E. variegatum, longitudinal section of rhizome. × 60.
FIG. 20. Same, section of sporophore and sporangia. × 60.
FIG. 21. E. variegatum var. Jesupi, longitudinal section of stem. × 40.
FIG. 22. Same, section of sporangium. × 250.
FIG. 23. E. hiemale, longitudinal section of rhizome. × 15.
FIG. 24. Same, section of sporangia. × 120.



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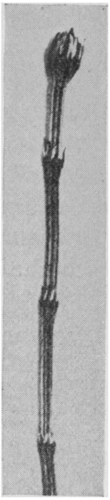

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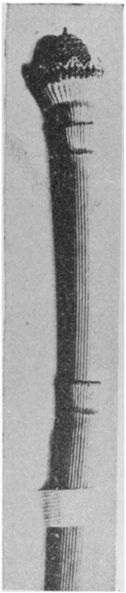

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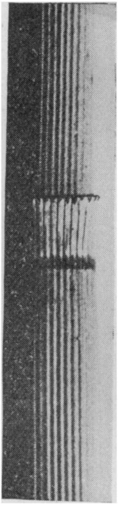

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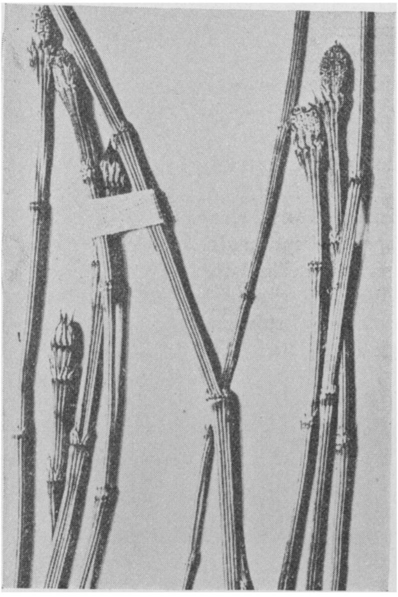

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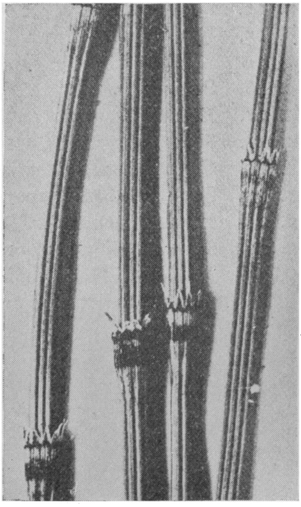

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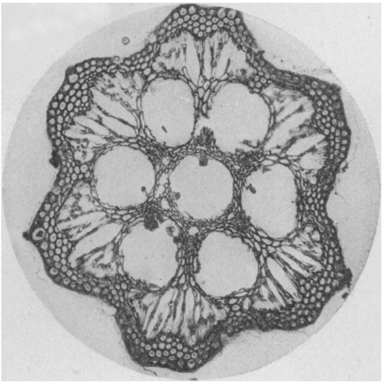
HOLDEN: ANATOMY OF A HYBRID EQUISETUM.



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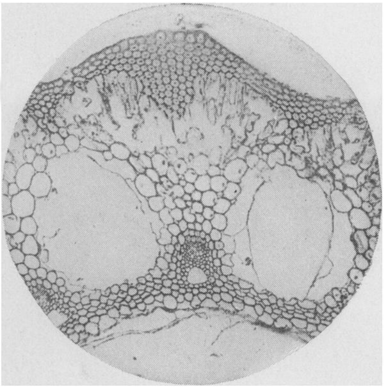

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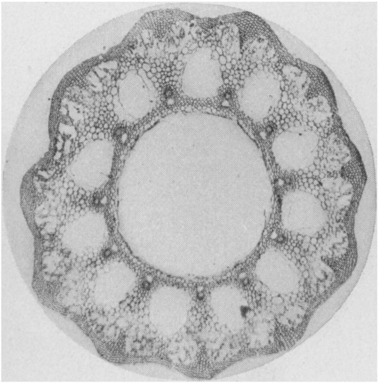

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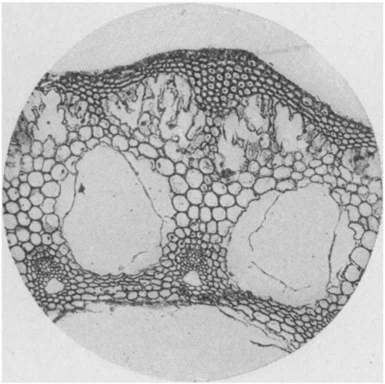

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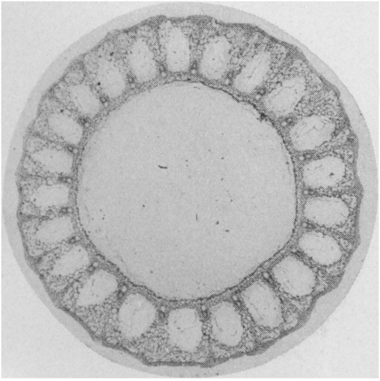

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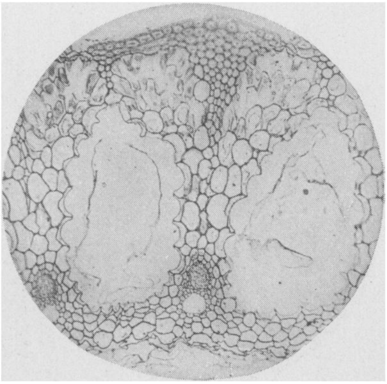

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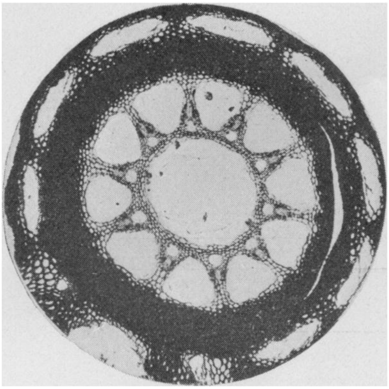

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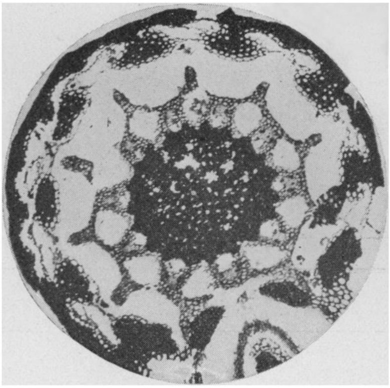

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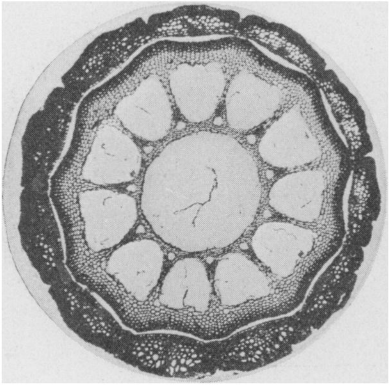

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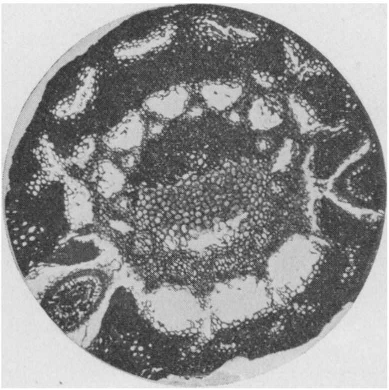

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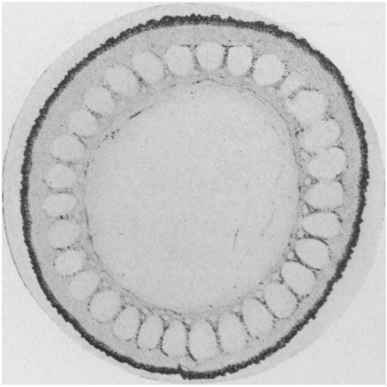

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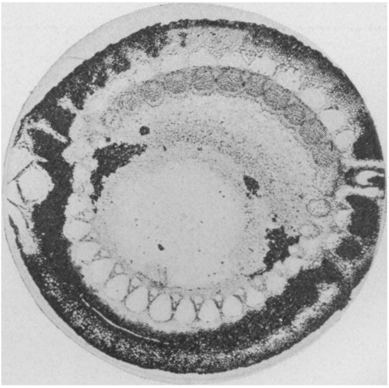

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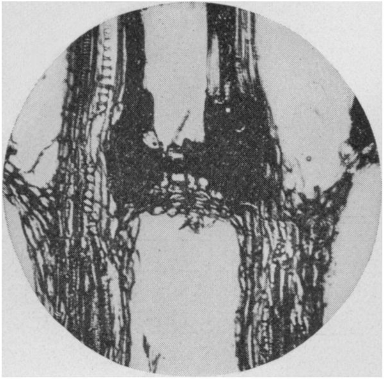

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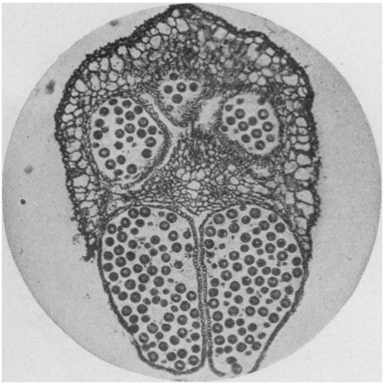

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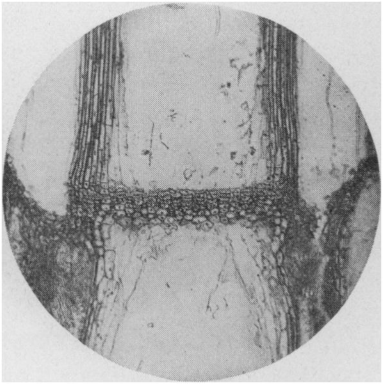

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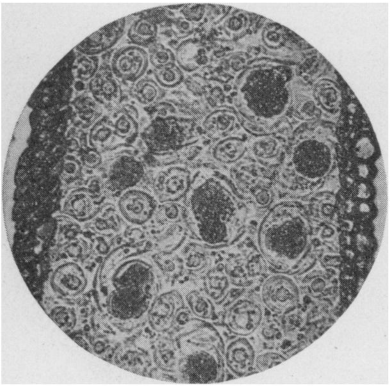

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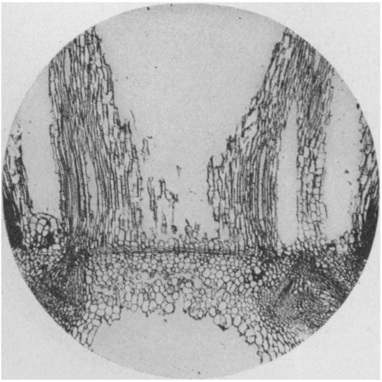

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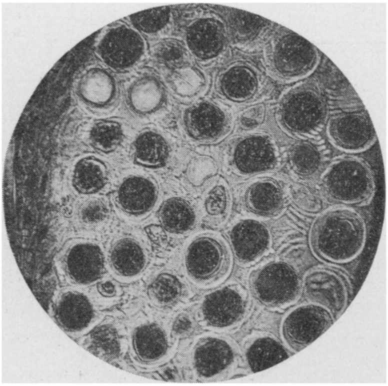

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HOLDEN: ANATOMY OF A HYBRID EQUISETUM.